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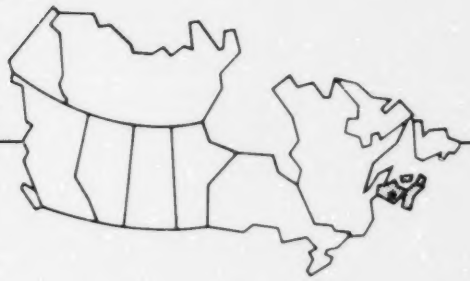
A selection index with desired gains to rogue jack pine seedling seed orchards

Y.S. Park, J.D. Simpson, D.P. Fowler, and E.K. Morgenstern



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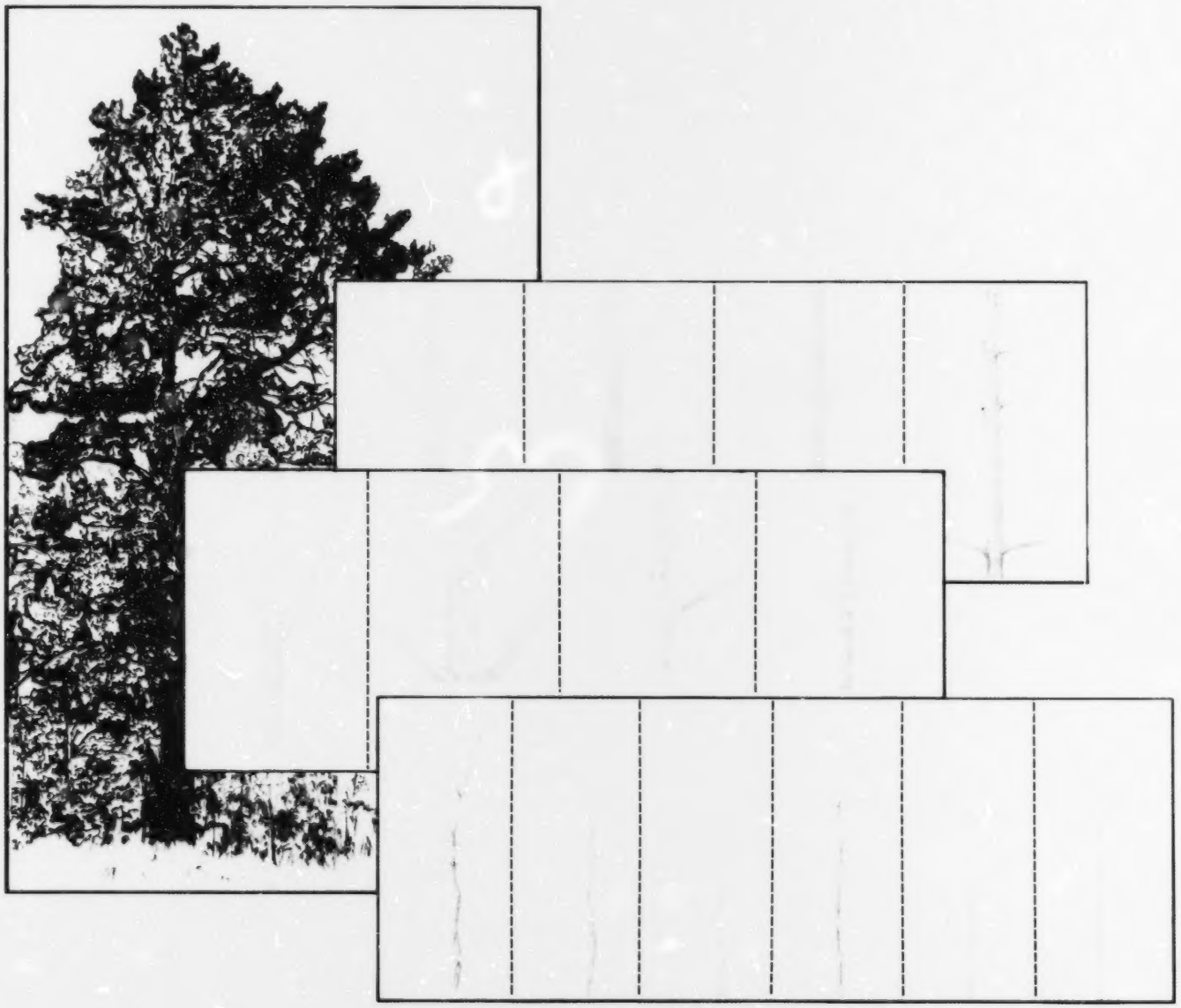

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A SELECTION INDEX WITH DESIRED GAINS TO ROGUE JACK PINE SEEDLING SEED ORCHARDS

by

Y.S. Park, J.D. Simpson, D.P. Fowler,
And E.K. Morgenstern[1]

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ABSTRACT

Jack pine (*Pinus banksiana* Lamb.) family tests at four locations in New Brunswick were evaluated at age 10 for height, diameter, volume, stem straightness, branch characteristics, and wood density. Significant variance due to families was found for all traits ranging from 3.4 to 10.0 percent of respective total phenotypic variance. Family x location interaction variance was small but significant for all traits except for wood density. There were negative genetic correlations between growth and quality traits, the largest of which was between volume and wood density (r = -0.706). A multi-trait selection index was developed, using volume, stem straightness, and branch characteristics for roguing families from seedling seed orchards. The index was based on the maximum gain in volume that could be attained while keeping stem straightness and branch characteristics at the population mean. Genetic gains at the suggested level of roguing, *i.e.*, retaining the 60 best families out of 164, were estimated as 7.6 percent of the overall mean for volume while stem straightness and branch characteristics remained unchanged.

RÉSUMÉ

On a étudié 6 traits (hauteur, diamètre, volume, rectitude du fût, caractéristiques des branches et densité du bois) de pins gris (*Pinus banksiana* Lamb.) de 10 ans faisant l'objet de tests de famille dans 4 stations du Nouveau Brunswick. On a constaté pour tous les traits des écarts significatifs imputables aux familles, soit de 3,4 à 10 % de la variance phénotypique totale de chacun. La variance de l'interaction entre la famille et la station était faible mais significative dans tous les cas sauf celui de la densité du bois. Les corrélations génétiques étaient négatives entre l'accroissement et la qualité, particulièrement dans le cas de la corrélation entre le volume et la densité du bois (r = -0,706). Le volume, la rectitude du fût et les caractéristiques des branches ont été utilisés pour constituer un indice de sélection multitraits permettant de rejeter les familles indésirables dans les vergers à graines. L'indice est fondé sur le gain maximum de volume qu'il est possible d'atteindre tout en conservant en moyenne un fût rectiligne et de bonnes caractéristiques des branches pour l'ensemble de la population. Au taux de rejet proposé, 104 familles sur 164, les gains génétiques sont estimés à 7,6 % de la moyenne générale sur le plan du volume, tandis que la rectitude du fût et les caractéristiques des branches demeurent inchangées.

Errata

The following errors have been discerned in M–X–176. The authors apologize for any inconvenience this may have caused.

Page i, column 2, line 23, should read 60 familles sur 164,

Page 1, column 1, line 7, should read substantial among and within provenance levels (Rudolf

Page 8, table 2, column 1, line 5, should read Plot, σ^2_p

Page 8, table 2, column 1, line 6, should read Within–plot, σ^2_w

Page 10, column 2, paragraph 3, line 23, omit ,wood density,

Page 10, column 2, G = should read

50.4794	-0.55772	-.48763
-0.55772	0.05960	+.00698
-.48763	+.00698	.04743

Page 11, Figure 5, omit G on the right–hand side above the horizontal axis.

Page 12, column 1, P = should read

66.12780	-0.54932	-0.57403
-0.54932	0.08130	0.01124
-0.57403	0.01124	0.06580

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INTRODUCTION

Jack pine (*Pinus banksiana* Lamb.) is second only to black spruce (*Picea mariana* (Mill.) B.S.P.) in importance as a reforestation species in New Brunswick. Current annual seedling production is about 10 million (Hallett, pers. comm.[2]). Genetic variation for economically important traits in jack pine is substantial at and within provenance levels (Rudolf and Yeatman 1982). Provenance information suggests that tree improvement programs in New Brunswick should concentrate on local materials. A program for jack pine, based on available genetic and biological information (Fowler 1986), was initiated by the New Brunswick Tree Improvement Council (NBTIC) in 1977.

Jack pine is a precocious species, capable of producing abundant male and female cones at about age 8, with cone production on seedlings exceeding that on grafts of comparable age (Rudolf and Yeatman 1982). A seedling seed orchard strategy for first generation improvement was therefore adopted by NBTIC. Eight hundred and fifty plus trees were selected in natural stands, based on height, stem straightness, and crown and branch characteristics (Coles 1979, Simpson 1988). Seeds collected from the selected trees were used to establish seedling seed orchards and family tests. This phase of the program, completed in 1987, was carried out over a ten-year period. The first series of family tests, established in 1979, was evaluated for growth and quality characteristics after 7 and 10 years from seed. The first seed orchard roguing was performed by removing the lower 40% of families using an index based on height, crown uniformity, branch angle and diameter, and stem straightness at 7 years (Adams 1988).

This report is based on results after 10 years. Its objectives are to 1) describe genetic variability for growth and quality traits, 2) examine genetic and phenotypic correlations among traits, 3) describe procedures for developing a selection index, and 4) make the second stage seed orchard roguing recommendations based on the selection index.

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[2]Hallett, R.D., Forestry Canada - Maritimes Region.

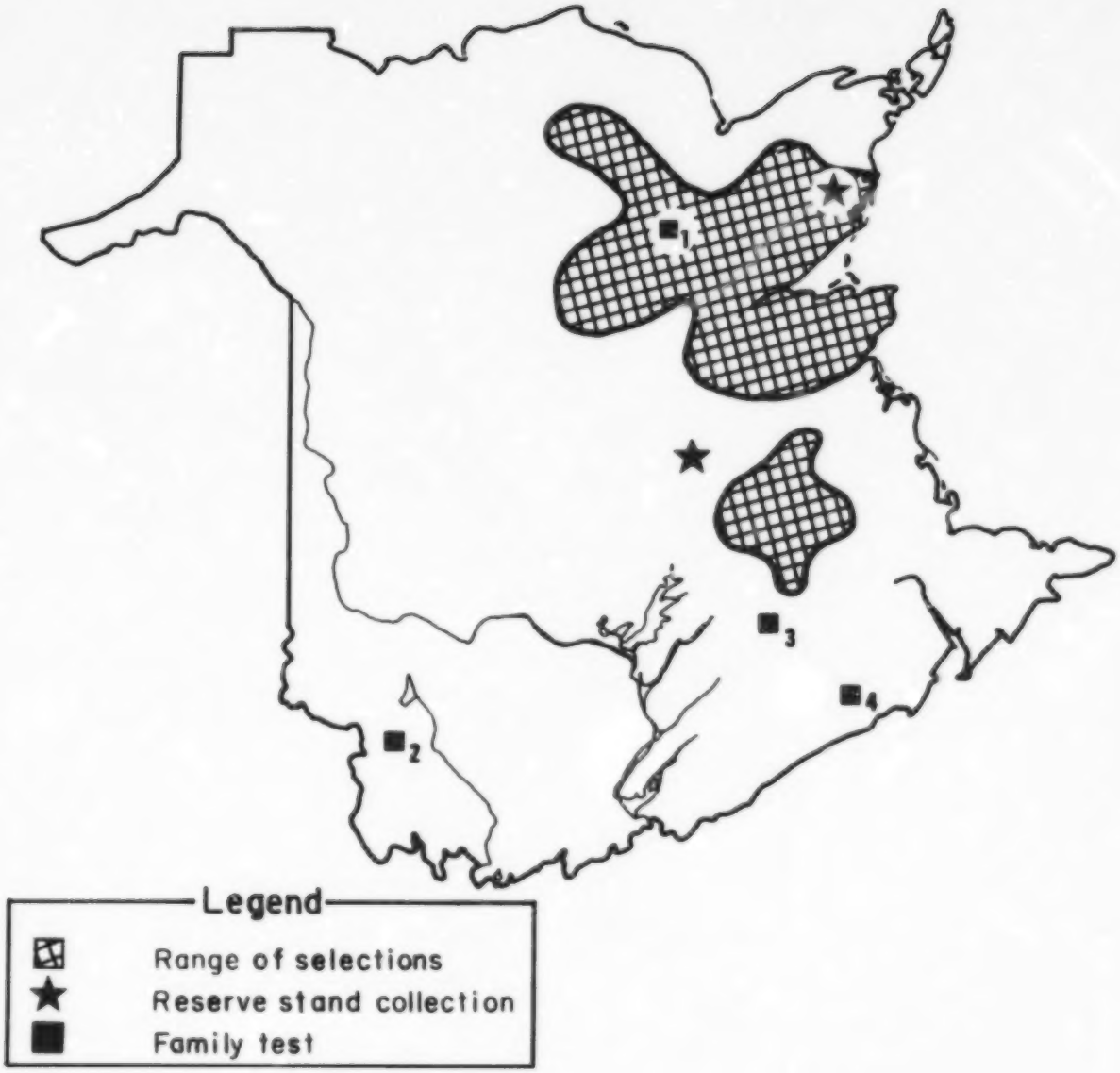

Figure 1. Map of New Brunswick showing the range of jack pine plus tree selections, location of reserve stand collections and family test locations: 1) Taylor Brook, 2) McAdam, 3) Dubee Settlement and 4) Donegal.

MATERIALS AND METHODS

Family tests and analyses

The material used in this family test series consisted of open-pollinated progenies from 162 plus trees selected in natural stands by NBTIC member agencies and 2 stand checks. In general, the best tree in a stand was selected, at an average selection intensity of approximately one tree per 5,000 examined. Areas explored for plus trees are shown in Fig. 1. Seedlings were raised in No. 608 Japanese paperpots (175 cm^3) by the Tree Improvement Unit at the Kingsclear Provincial Forest Nursery during the winter of 1979. In the spring of 1979, field tests were established at four locations in New Brunswick (Fig. 1): Taylor Brook by the New Brunswick Department of Natural Resources, McAdam by Georgia-Pacific Corp., Dubee Settlement by J.D. Irving Ltd., and Donegal by MacMillan Rothesay Ltd. The test areas were site-prepared cutovers. At each test location, families were planted in 4-tree-row plots in ten randomized blocks.

At the end of the tenth growing season (1988), total height and diameter at breast height were measured to the nearest centimeter and millimeter, respectively. Tree volume (VO) was computed using a volume equation in m^3 for jack pine derived by Honer *et al.* (1983). The volume estimates were multiplied by 10^7 in the analyses because the computed volume figures in m^3 were too small to carry a sufficient number of significant digits. The estimates, however, may not be considered as absolute values, because small trees were not included in the data set used to generate the volume equation. Thus, they should be treated as relative volume estimates. Quality characteristics were evaluated using subjective scores. Stem straightness (ST) was scored on a 1 (worst) to 6 (best) scale (Fig. 2) taking into consideration the degree of sweep, crook, and lean by evaluating trees from two planes, *i.e.*, 90° to each other. Branch angle (Fig. 3) and branch diameter (Fig. 4) scores ranged from 1 to 4 (worst to best). A composite branch characteristics score (BR) was obtained by adding branch angle and diameter scores, and thus ranged from 2 to 8. Wood density (WD) was estimated from the depth of pin penetration using a Pilodyn wood tester model "Forest" with an injection energy of 6 joules and a pin of 2.5 mm diameter and 80 mm length. The measurements were made on three trees of each family in three blocks at three test locations, excluding Taylor Brook. The Pilodyn readings were converted to green wood density using a regression equation ($R^2 = 0.58$), WD = 0.479863 - (0.0075787P), where P is the Pilodyn reading. The equation was developed from a sample of 47 trees of the same age by regressing densities obtained by the water displacement method (Olesen 1971) on Pilodyn readings (Villeneuve 1986).

Analyses of variance and covariance were performed to obtain genetic parameters. Since the data were unbalanced due to missing observations, two analyses were carried out (Kempthorne 1969). One analysis of variance was for between and within plots using individual tree data. The model used was:

$$Y_{ij} = \mu + P_i + w_{ij},$$

where

- Y_{ij} is the j-th observation in the i-th plot;
- μ is the overall mean;
- P_i is the i-th plot effect; and
- w_{ij} is the random error associated with individuals.

The other analysis of variance was based on plot means using the model:

$$Y_{ijk} = \mu + L_i + R_{ij} + F_k + LF_{ik} + E_{ijk},$$

where

- Y_{ijk} is the plot mean for the k-th family in the j-th block within the i-th location;
- μ is the overall mean;
- L_i is the i-th location effect;
- R_{ij} is the j-th block effect within i-th location;
- F_k is the k-th family effect;
- LF_{ik} is the interaction effect between the i-th location and k-th family; and
- E_{ijk} is the random error component.

All terms in the analyses were considered as random effects and computations were carried out using SAS (1982). Since variance on individuals was available, plot error variance (σ^2_p) was estimated noting the following relationship,

$$\sigma^2_E = \sigma^2_p + nh\,\sigma^2_w,$$

where

- σ^2_E is the error variance from analyses based on plot means;

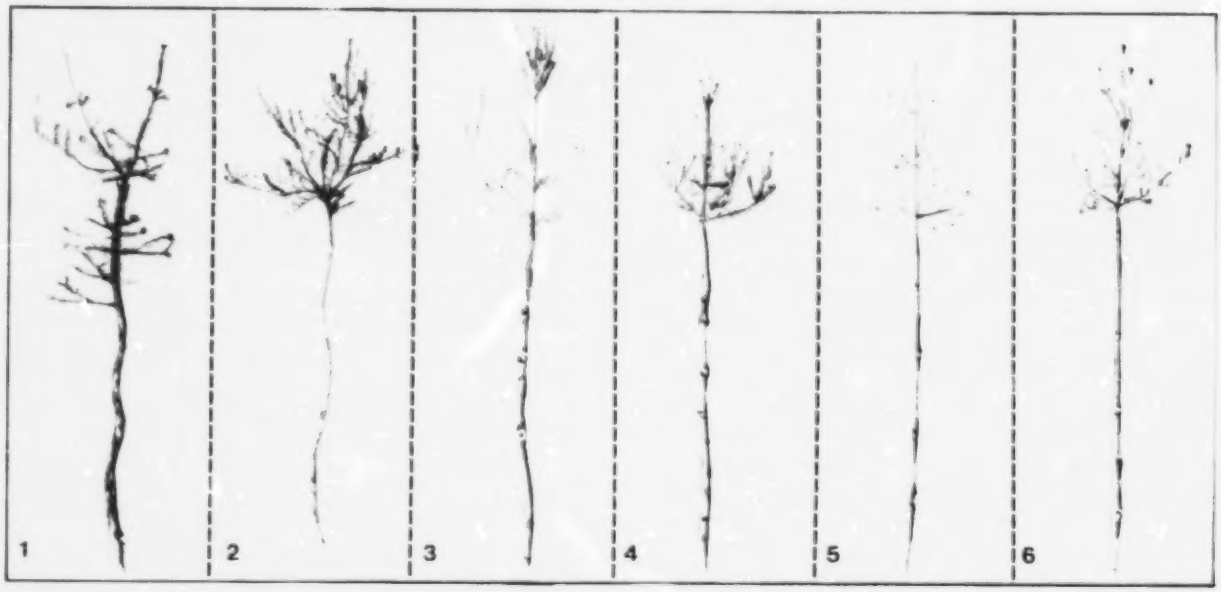

Figure 2. Stem straightness scores: 1) great deal of crook in two planes; 2) great deal of crook in one plane or considerable crook in two planes; 3) considerable crook in one plane or moderate crook in two planes; 4) moderate crook in one plane or slight crook in two planes; 5) slight crook in one plane only; and 6) no crook or very slight crook in one plane only.

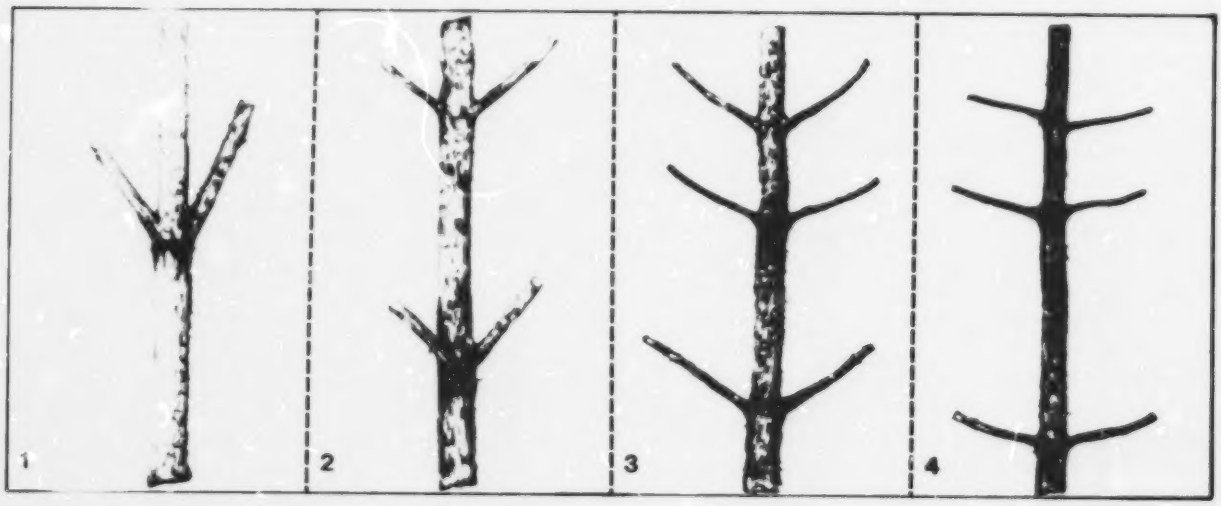

Figure 3. Branch angle scores: 1) branches emerging from stem at very acute angle <30°; 2) branches emerging from stem at 30°-45°; 3) branches emerging from stem at 46°-65°; and 4) branches emerging from stem at very flat angle, >65°.

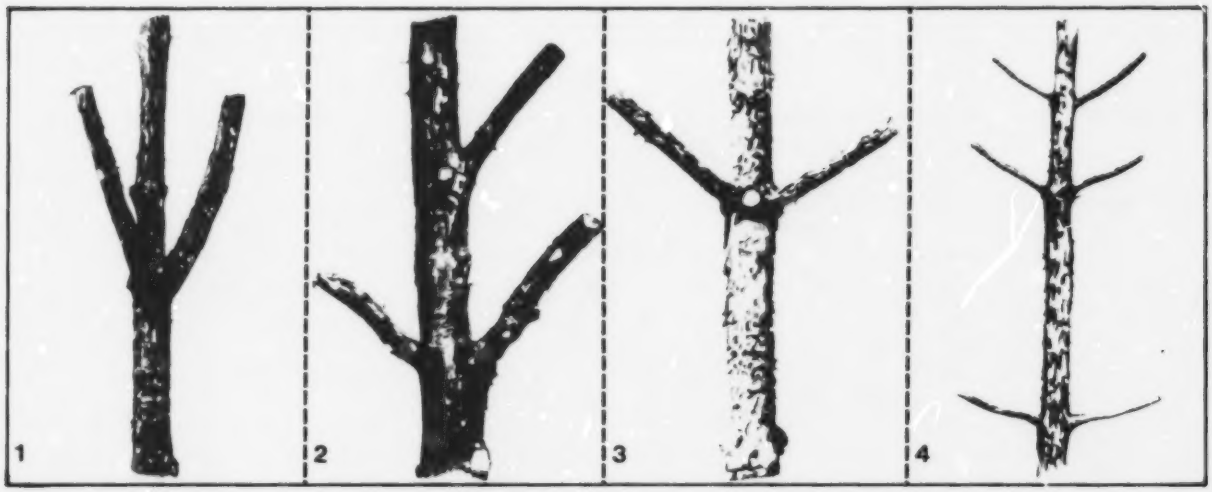

Figure 4. Branch diameter scores: 1) very coarse branching relative to bole size (>50%); 2) moderate to coarse branch size relative to bole size (41-50%); 3) fairly fine to moderate branching relative to bole size (31-40%); and 4) very fine branching relative to bole size (<30%).

nh is the reciprocal of harmonic means of the number of trees per plot mean; and

σ^2_w is the within-plot error variance based on individuals.

The form of analyses of variance and covariance is presented in Table 1. Variance and covariance components were estimated by equating expected mean squares or mean cross products to calculated mean squares or cross products and solving for the components. Standard deviations of the estimated components were calculated as given by Kempthorne (1969):

$$sd(\sigma^2_i) = [\ \Sigma\ \{\ 2 \cdot k_i^2 \cdot (MS_i)^2/(df_i + 2)\}\ ]^{1/2},$$

where

$sd(\sigma^2_i)$ is the standard deviation of the i-th estimated variance component;

k_i is the coefficient of the linear combination of mean squares;

MS_i is the mean squares used to estimate the component; and

df_i is the respective degrees of freedom for the mean squares.

The estimated variance components were interpreted in terms of genetic and environmental variances and were used in deriving various genetic parameters.

Narrow-sense heritability based on individuals (h^2_I), from open-pollinated families was estimated as:

$$h^2_I = 4 \cdot \sigma^2_F / (\sigma^2_w + \sigma^2_p + \sigma^2_{LF} + \sigma^2_F),$$

where

σ^2_F is the variance component due to families (see Table 1 for explanation of the remaining terms).

The heritability for family means (h^2_F) was estimated as:

Table 1. Form of analyses of variance and covariance[1]

Source	D.F.	Expected mean squares (cross-products[1])
Locations (L)	3	$0.317\ \sigma^2_W + \sigma^2_P + 9.669\ \sigma^2_{LF} + 0.922\ \sigma^2_F + 137.140\ \sigma^2_B + 1371.053\ \sigma_L{}^2$
Blocks in L (R)	36	$0.317\ \sigma^2_W + \sigma^2_P + 0.036\ \sigma^2_{LF} + 0.036\ \sigma^2_F + 137.171\ \sigma^2_B$
Families (F)	163	$0.317\ \sigma^2_W + \sigma^2_P + 9.659\ \sigma^2_{LF} + 33.417\ \sigma^2_F$
L x F	403	$0.317\ \sigma^2_W + \sigma^2_P + 9.609\ \sigma^2_{LF}$
R x F	5486	$0.317\ \sigma^2_W + \sigma^2_P$
Within plot	13504	σ^2_W

where σ^2_W, σ^2_P, σ^2_{LF}, σ^2_F, σ^2_B, and σ^2_L are variance components due to within-plot, plot, location x family interaction, family, block, and location, respectively.

[1]For analysis of covariance between traits x and y, the variance components in the above Table are replaced by corresponding covariance components, i.e., $\sigma_W(xy)$, $\sigma_P(xy)$, $\sigma_{LF}(xy)$, $\sigma_F(xy)$, $\sigma_B(xy)$, and $\sigma_L(xy)$, which are covariance components due to within-plot, plot, location x family interaction, family, block, and location, respectively. Analyses involving wood density have a similar analysis form since the same models were used, but the sample size varied.

$$h^2_F = \sigma^2_F / (0.009 \cdot \sigma^2_W + 0.030 \cdot \sigma^2_P + 0.289 \cdot \sigma^2_{LF} + \sigma^2_F).$$

The denominator was obtained by dividing the expected mean square for families by the coefficient for the component due to families.

Relationships among the traits were examined using genetic and phenotyic correlations. Genetic correlations were computed as in Falconer (1960):

$$r_g(xy) = \sigma_F(xy) / [\ \sigma^2_F(x) \cdot \sigma^2_F(y)\ ]^{1/2},$$

where

- $r_g(xy)$ is the genetic correlation between traits x and y;
- $\sigma_F(xy)$ is the component of covariance due to families between traits x and y; and
- $\sigma^2_F(x)$ and $\sigma^2_F(y)$ are the variance components due to families for traits x and y, respectively.

Similarly, phenotypic correlations based on family means were computed as:

$$r_p(xy) = \sigma_{pf}(xy) / [\ \sigma^2_{pf}(x) \cdot \sigma^2_{pf}(y)\ ]^{1/2},$$

where

- $r_p(xy)$ is the phenotypic correlation based on family means for traits x and y;
- $\sigma_{pf}(xy)$ is the phenotypic covariance based on family means for traits x and y, obtained by dividing the expected cross-product for family by the coefficient of covariance component for family; and
- $\sigma^2_{pf}(x)$ and $\sigma^2_{pf}(y)$ are the phenotypic variances of family means for traits x and y, res-

pectively, as in the denominator of heritabilty based on family means.

Heritabilities for individual traits are used to predict genetic gains from selection. Expected genetic gain is:

$$\Delta G = i \cdot h^2 \cdot \sigma,$$

where

- ΔG is expected genetic gain for the trait in question;
- i is the selection intensity;
- h^2 is the appropriate heritability depending on the selection method; and
- σ is the corresponding phenotypic standard deviation.

Selection for one trait (x), however, will result in correlated response in other traits (y) which can be predicted as:

$$\Delta R(y) = i \cdot h(x) \cdot h(y) \cdot r_g(xy) \cdot \sigma(y),$$

where

- $\Delta R(y)$ is the correlated response of trait y due to selection in trait x;
- $h(x)$ and $h(y)$ are the square roots of appropriate heritabilities for traits x and y, respectively; and
- $\sigma(y)$ is the corresponding phenotypic standard deviation for the trait y.

Index selection

Index selection is the most efficient form of multi-trait selection. For simultaneous improvement of several traits, the method provides an index score so that selection is equivalent to single trait truncation selection. The theory of the selection index was first developed by Smith (1936), and later by Hazel and Lush (1942). The selection index (**I**) is defined, in matrix notation, as:

$$\mathbf{I} = \mathbf{x'b},$$

where **x** is a known vector of phenotypic values for the traits and **b** is an unknown vector of index coefficients to be calculated. The solution for **b** is given by the expression:

$$\mathbf{b} = \mathbf{P}^{-1}\,\mathbf{G}\,\mathbf{a},$$

where **P** and **G** are phenotypic and genotypic variance-covariance matrices, respectively, and **a** is a vector of known economic weights. The genetic gain using selection based on the index (**I**) is:

$$\Delta = \mathbf{G}\,\mathbf{b}\,(i/\sigma_I),$$

where Δ is the vector of genetic gains of individual traits used in the index equation, i is selection intensity, and σ_I is the standard deviation of the index, *i.e.*,

$$\sigma_I = (\mathbf{b'}\,\mathbf{P}\,\mathbf{b})^{1/2}.$$

Index selection requires accurate estimates of genetic and phenotypic variances and covariances, as well as economic weights for the component traits. Despite its many optimal properties, index selection has not been widely used because of the difficulty in obtaining economic weights for various traits in forest trees. Several modifications have been proposed (see Lin (1978) for review). The methods of 'restricted' selection indices of Kempthorne and Nordskog (1959), Tallis (1962), Harville (1975), and Tai (1977) are among the most widely applied modifications in plant and animal breeding. Other modified indices include a base index, where relative economic weights are used as index coefficients (Williams 1962), and a weight-free index based on observed phenotypic values (Elston 1963).

The restricted selection index method of Kempthorne and Nordskog (1959) is designed to change the response of some traits while holding the response of other traits to zero. Tallis (1962) further extended the restricted index by providing a method of setting the response of some traits at a fixed amount while maximizing genetic gain in other traits. Similarly, Pesek and Baker (1969), in considering the problem of assigning ecomonic weights, proposed an index designed to attain pre-specified levels of genetic gain for each of the traits used in the index equation. The index coefficient (**b**) for this index can be derived from the gain equation as:

$$\mathbf{b} = \mathbf{G}^{-1}\,\Delta,$$

since i/σ_I is a constant which was dropped. Thus, this procedure eliminates the necessity of estimating relative economic weights and the phenotypic variance-covariance matrix. The restricted index approach of Pesek and Baker (1969) was used here for selection based on mean performance of families.

Table 2. Estimated variance components with standard deviation in parentheses, for height, diameter, and volume, their percentage of total variance, individual (h^2_I) and family mean (h^2_F) heritabilities and trait means.

Variance Component for		Height			Diameter			Volume[1]		
		Estimate		%	Estimate		%	Estimate		%
Location(L),	σ^2_L	2706.9	(1730.8)	-	0.357	(0.231)	-	486.0	(313.6)	-
Blocks,	σ^2_B	284.7	(67.2)	-	0.090	(0.022)	-	93.1	(22.0)	-
Family(F),	σ^2_F	179.5	(24.4)	6.4	0.054	(0.009)	3.4	50.5	(7.4)	4.7
L x F,	σ^2_{LF}	24.2	(10.2)	0.9	0.015	(0.006)	0.9	13.8	(3.9)	1.3
Plot,	σ^2_P	436.8	(24.2)	15.6	0.147	(0.013)	9.2	104.3	(8.6)	9.8
Within-plot,	σ^2_F	2162.8	(26.3)	77.1	1.382	(0.017)	86.5	900.8	(11.0)	84.2
Total[2]	σ^2_T	2803.3		100.0	1.598		100.0	1069.4		100.0
Heritability:										
individual,	h^2_I	0.26			0.14			0.19		
family mean,	h^2_F	0.81			0.71			0.76		
Mean		423.3			6.5			72.4		

[1]Volume in m^3 multiplied by 10^7.

[2]Total phenotypic variance of individuals, *i.e.*, $\sigma^2_T = \sigma^2_W + \sigma^2_P + \sigma^2_{LF} + \sigma^2_F$.

RESULTS AND DISCUSSION

Estimated variance components and heritabilities for each trait are presented in Tables 2 and 3. All variance components, except those for location x family interactions in wood density, were significant at the 5% probability level. The environmental sources of variation, *i.e.*, variance components due to location (σ^2_L) or blocks within a location (σ^2_B), were large for all traits and exceeded the variance component due to families (σ^2_F). The genetic source of variation estimated by σ^2_F ranged from 3.4 - 10% of total phenotypic variance for all traits. This component is translated into covariance of half-sibs, and is interpreted as approximately one-quarter of additive genetic variance (σ^2_A). Genotype x environment interaction variance (σ^2_{LF}) was small but significant for most traits, ranging from 0.9 - 1.5% of total phenotypic variation. The largest variation was due to tree-to-tree variation within plots (σ^2_W) ranging from 77.2 - 91%. Narrow-sense heritability of individuals ranged from 0.14 to 0.40, while the heritability of family means ranged from 0.67 to 0.81.

Genetic and phenotypic correlations computed from estimated components of variance and covariance are presented in Table 4. The growth traits, *i.e.*, height, diameter, and volume, were negatively correlated with quality traits, *i.e.*, stem straightness, branch characteristics, and wood density. It follows that selection for rapid growth will result in decreased quality. The largest negative correlation was found between volume and wood density with r =-0.706, implying that selection for one of these traits could have an impact on the other. This correlation for jack pine is much larger than that reported for 15-year-old jack pine with r = 0.01 using

Table 3. Estimated variance components with standard deviation in parentheses, for stem straightness (ST), branch characters (BR), and wood density (WD), their percentage of total variance, individual (h^2_I) and family mean (h^2_F) heritabilities and trait means.

Variance Component for	Stem Straightness			Branch Characters			Wood density[1]		
	Estimate		%	Estimate		%	Estimate		%
Location(L), σ^2_L	0.545	(0.347)	-	0.041	(0.031)	-	0.219	(0.165)	-
Blocks, σ^2_B	0.031	(0.008)	-	0.074	(0.018)	-	0.035	(0.021)	-
Family(F), σ^2_F	0.060	(0.009)	4.0	0.047	(0.007)	3.6	0.237	(0.040)	10.0
L x F, σ^2_{LF}	0.022	(0.005)	1.5	0.019	(0.005)	1.4	-0.30	(0.029)	0.0
Plot, σ^2_p	0.096	(0.011)	6.5	0.052	(0.010)	4.0	0.269	(0.050)	11.2
Within-plot, σ^2_w	1.304	(0.016)	88.0	1.201	(0.015)	91.0	1.880	(0.054)	78.8
Total[2] σ^2_T	1.481		100.0	1.319		100.0	2.386		100.0
Heritability:									
individual, h^2_I	0.16			0.14			0.40		
family mean, h^2_F	0.73			0.72			0.67		
Mean	3.6			5.7			0.338		

[1]Estimates multiplied by 10^3.

[2]See footnote in Table 2.

Table 4. Genotypic (upper triangle) and phenotypic (lower triangle) correlations among traits for ten-year-old jack pine families.

	Height	Diameter	Volume	Stem	Branch	Density
Height		0.803	0.892	-0.309	-0.298	-0.414
Diameter	0.790		0.990	-0.305	-0.270	-0.684
Volume (VO)	0.875	0.970		-0.322	-0.315	-0.706
Stem (ST)	-0.210	-0.226	-0.237		0.131	0.132
Branch (BR)	-0.246	-0.275	-0.275	0.154		0.038
Density (WD)	-0.309	-0.552	-0.554	0.160	0.128	

increment cores (Ernst *et al.* 1983), loblolly pine (*Pinus taeda* L.) with r =-0.068 using wood disk samples (Bridgwater *et al.* 1983) and r =-0.53 for diameter and wood density of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) (King *et al.* 1988) based on pilodyn readings. Also, this correlation is larger than that of volume and density for 20-year-old jack pine (r =-0.05) based on disks at Petawawa National Forestry Institute (Magnussen, pers. comm.)[3]. Obviously, our estimated correlation is inflated. Using pilodyn readings and converting them into wood density using a regression equation with a low R^2 value was the major cause of this inflated estimate. Using a regression model to obtain a non-measured trait from a regressor reduces the phenotypic variance, and the correlation becomes inflated (Magnussen, pers. comm.)[3]. The correlations between growth traits and stem straightness and branch characteristics were smaller than those with wood density, ranging from -0.322 to -0.270, but were still large enough to have a considerable impact on the selected population.

The above data are required to develop recommendations for roguing seed orchards, which, when combined with the previous roguing, will result in removal of the lower 64% of the families at a selection intensity of 1.02 (Becker 1984). Several indices were considered using the four traits, volume, wood density, stem straightness, and branch characteristics.

Volume is the most important commercial trait, but relative economic weight is not readily available. In the absence of such weight, emphasis was placed on volume while restricting responses of quality characteristics to a constant level. Pesek and Baker's (1969) approach of specifying the relative amount of desired gain for each trait was adopted; however, the strong negative genetic correlation between volume and wood density poses a problem in assigning optimum proportional gains. Thus, the response to selection in volume and wood density under varying selection schemes was examined (Fig. 5). Family selection, based on volume alone, and at an intensity of 1.02, would result in a gain of 8.76% of the mean volume, but the correlated response in wood density would amount to a 0.91% reduction in mean wood density. Similarly, the correlated responses for stem straightness and branch characteristics were -1.95% and -1.07%, respectively. As the emphasis on wood density increases, a drastic reduction in volume results. Selection for wood density alone would provide a 1.21% gain, but the correlated loss in volume would be 6.10%. If gain in wood density is held at zero, volume gain is almost halved (from 8.76% to 5.12%). Despite its sizable heritability, the selection response of wood density is small, ranging from -0.91 to 1.21%, while that of volume is relatively large, ranging from -6.10 to 8.76%.

Due to the great impact of this negative correlation, we were prepared to accept some decline in wood density when constructing an index for family selection. Since individual tree heritability in wood density is large, it is anticipated that substantial gain can be achieved when within-family selection is conducted to select trees in the family tests for the second generation improvement efforts.

To develop the index it is necessary to specify the desired gain for each trait. Although any weight (or restriction) can be assigned in the index, it must be biologically realistic. For example, with a strong negative genetic and phenotypic correlation between VO and WD, it is unrealistic to attempt to maximize gain in both traits. It was decided that VO should be maximized, a small decline in WD would be accepted, and ST and BR would be held at the current level. As a procedure for assigning proper weights for VO and WD, the maximum possible genetic gain in VO and the correlated response in WD were examined using the equations introduced earlier. At a selection intensity of 1.02 the maximum possible gain in VO is 6.332 (0.063 m^3) with a correlated response in WD of -0.0031 kg/m^3. These can be considered the limits for genetic gain. It was decided that this level of decline in WD was acceptable, and excluded from the index. Thus, the index was developed maximizing gain for VO, while holding the weights for ST and BR at zero, *i.e.*, $\Delta' = [1, 0, 0]$. The genotypic (**G**) and phenotypic (**P**) variance covariance matrices for volume, wood density, stem straightness, and branch characteristics, respectively, were:

$$\mathbf{G} = \begin{bmatrix} 50.49740 & -0.02443 & -0.55772 \\ -0.02443 & 0.00002 & 0.00016 \\ -0.55772 & 0.00016 & 0.05960 \end{bmatrix}$$

and

[3]Magnussen, S., Forestry Canada, Petawawa National Forestry Institute.

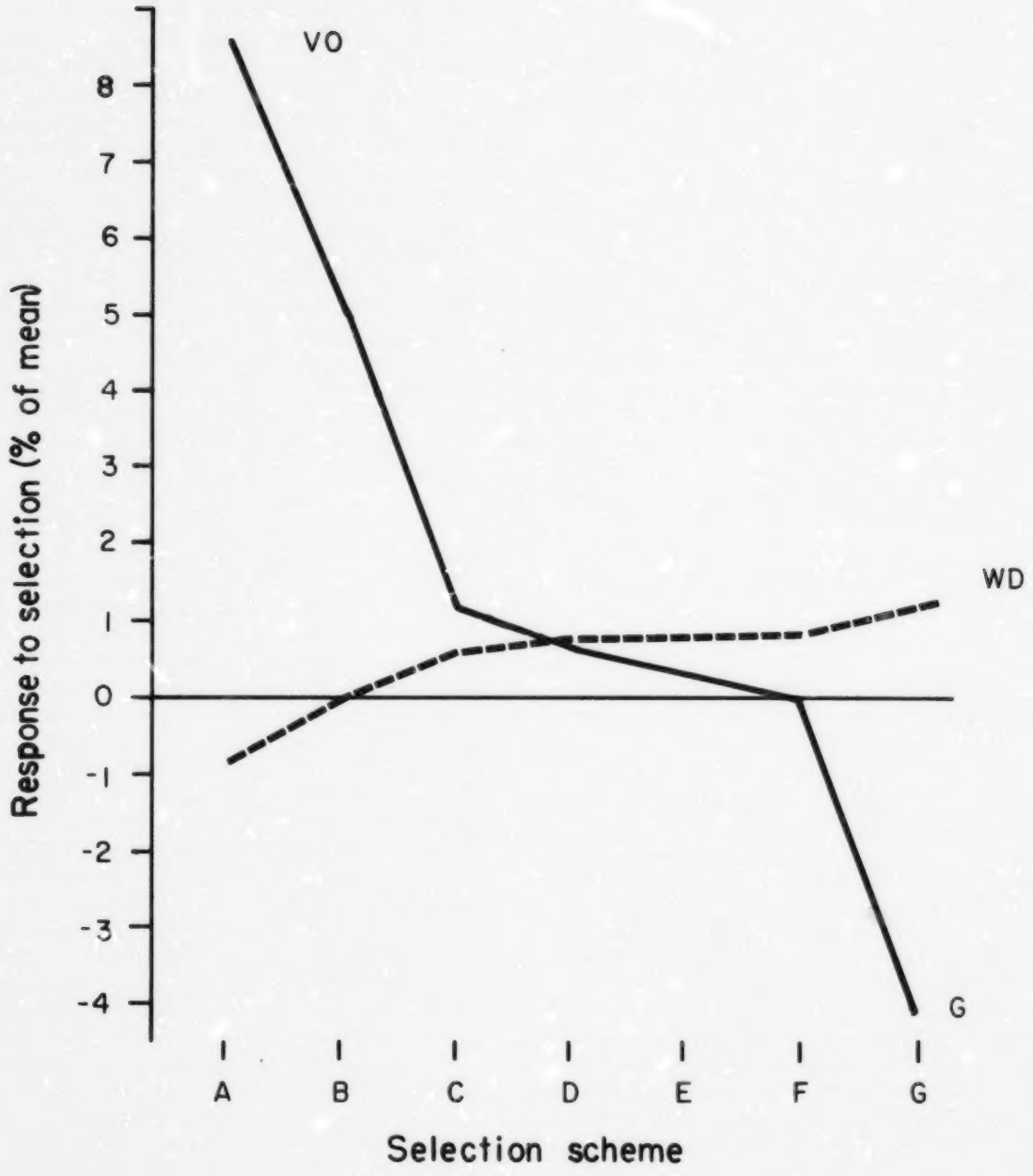

Figure 5. Response to selection in volume (VO) and wood density (WD) as percent of mean under varying selection schemes: **A.**Selection for VO alone with correlated response in WD; **B.** Index selection maximizing gain in VO while holding gain in WD at zero; **C.** Index selection emphasizing desired gain in VO and WD by 2:1, respectively; **D.** Index selection with an equal emphasis on VO and WD; **E.** Index selection emphasizing WD and VO by 2:1, respectively; **F.** Index selection maximizing WD while holding VO at zero; and **G.** Selection for WD with correlated response in VO.

$$\mathbf{P} = \begin{matrix} 66.12780 & -0.02685 & -0.54932 \\ -0.02685 & 0.00003 & 0.00027 \\ -0.54932 & 0.00027 & 0.08131 \end{matrix}$$

The vector of index coefficients, $\mathbf{b}' = [0.02414, 0.20025, 0.2187]$ was obtained by using the expression, $\mathbf{G}^{-1}\Delta$. Thus, the index equation is:

I = 0.02414 (volume) + 0.20025 (stem straightness) + 0.2187 (branch characteristic).

To obtain index scores for each family, family means for each trait were computed, after adjusting for location and block effects, and were substituted in the equation. The adjustment was necessary due to large differences among the test locations and to unequal family representation among these locations. For example, an unadjusted family mean would be biased upwardly if it was represented only on the most productive site. The adjusted data for each trait were obtained by:

$$Y_{ijk} = U_{ijk} - Y_{ij.} + Y_{...},$$

where

Y_{ijk} and U_{ijk} are the adjusted and unadjusted plot means of the k-th family in the j-th block of the i-th location, respectively;

$Y_{ij.}$ is the j-th block mean in the i-th location; and

$Y_{...}$ is the overall mean.

The families were ranked on the basis of index scores and truncation selection was carried out leaving the best 60 families. Theoretical gain for volume based on this index is estimated as 7.6% of the overall mean, while maintaining stem straightness and branch characteristics at zero. Incidentally, selection differentials, *i.e.*, the difference between mean of the selected portion of the population and that of the entire population, due to index selection for each trait as a percent of respective trait means, were 5.33% for index score, 2.86% for height, 4.02% for DBH, 10.58% for VO, 1.12% for ST, 0.43% for BR, and -0.68% for WD.

The efficiency of any selection index is dependent on the accuracy of the estimated genetic parameters, *e.g.*, variance-covariance matrices. Tai (1986) points out that it is important to test a large sample of genotypes to ensure high precision of the estimates of response to multi-trait selection. The number of families included in this test is 164, which should be sufficiently large. Hayes and Hill (1980) provided a method of examining sampling properties of such matrices and recommended a linear transformation. This transformation finds new variables which have phenotypic variances of 1 and genotypic variances equal to the eigenvalue, λ, of the determinantal equation, $\mathbf{G} - \lambda\mathbf{P} = 0$, with all covariances of zero. According to this method, if any of the eigenvalues are negative, this indicates that some of the partial genotypic correlations exceed the acceptable range of -1 to +1 on the untransformed scale. Also, if the eigenvalues exceed 1.0, then there is an indication that some of the partial environmental correlations exceed the acceptable range of -1 to +1. Thus, this method provides a means of inspecting the validity of estimated parameters. The set of eigenvalues in our data was $\lambda = [0.8016, 0.7380, 0.6362]$, which falls into the acceptable range.

The relationships between family rankings based on the current (Index 10) and the 7-year (Index 7) indices, as well as with the other 10-year growth and quality traits, are presented in Table 5. As previously mentioned, the index used for first roguing was based on evaluation of height, crown uniformity, stem straightness, and branch angle and diameter at seven years, using the 118 families represented at all four locations (Adams 1988). Based on the common 118 families, the correlation with Index 10 was 0.741. Although this is a significant correlation, substantial rank changes still occur (see APPENDIX I). As expected, Index 10 had the largest correlation with volume ($r = 0.907$), however, the correlation with DBH ($r = 0.877$) was almost as large. If the selection goal is to improve volume, it is essential that data on diameter be available. Although height is strongly correlated with both volume and the index ($r = 0.797$), it is not as reliable an indicator of volume. Also, the index rankings of the two reserve stand check lots included in this test series were 105th and 128th. Although these reserve stands were phenotypically selected for interim seed collection, their performance in the family tests falls well below that of selected families.

Increased volume production of future plantations is a goal of the NBTIC tree improvement program. Recognizing that there are other traits such as stem straightness or wood density which can influence future product values, it is important that they receive careful attention through index selection strategy. Although the restricted selection index used here can provide an effective means of

Table 5. Correlation coefficients among current index score (Index10) with the index ranking based on 7-year evaluation (Index7[a]), height at age 7 (HT7) and growth and quality traits at age 10.

	2 Index7	3 HT7[b]	4 HT10	5 DBH	6 VO	7 ST	8 BR	9 WD
1. Index10	0.741	0.640	0.797	0.877	0.907	0.101	0.052	-0.312
2. Index7		0.629	0.685	0.634	0.697	0.024	0.042	-0.306
3. HT7			0.773	0.664	0.726	-0.242	-0.188	-0.237
4. HT10				0.797	0.881	-0.209	-0.243	-0.263
5. DBH					0.966	-0.207	-0.281	-0.348
6. VO						-0.232	-0.274	-0.373
7. ST							0.180	0.175
8. BR								0.112

[a]Index developed by Adams (1988).
[b] Adjusted for site-block effects.
Absolute correlation coefficients larger than 0.112 are significant at $p = 0.05$.

seed orchard roguing, it will be necessary in the future to have accurate economic weights for each trait to fully determine the aggregate genetic worth of the families.

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APPENDIX I. Family rankings in descending order of ten-year index score (R10) with seven-year index rankings (R7) and means of growth and quality characters

Family	Index	R10	R7[1]	HT10	DB	VO	ST	BR	WD
01-172	4.39738	1	·	470.1	7.05	103.26	3.30	5.69	0.3371
01-171	4.27184	2	·	454.7	6.93	97.33	3.54	5.55	0.3277
01-184	4.14477	3	3	455.6	6.84	91.45	3.44	5.71	0.3236
01-126	4.14140	4	·	444.1	6.62	82.73	3.84	6.29	0.3509
01-118	4.09470	5	·	444.2	6.73	85.10	4.13	5.55	0.3293
01-117	4.09244	6	·	441.6	6.88	88.74	3.44	5.77	0.3398
01-177	4.08891	7	4	449.9	6.70	87.21	3.77	5.62	0.3355
01-180	4.06186	8	10	439.5	6.77	88.47	3.44	5.66	0.3298
01-016	4.03801	9	1	460.1	6.38	79.33	4.04	6.01	0.3347
01-134	4.02530	10	13	442.3	6.70	85.46	3.74	5.55	0.3321
01-179	4.00284	11	·	442.9	6.55	85.50	3.23	5.91	0.3340
01-191	4.00152	12	·	443.4	6.85	88.20	3.28	5.56	0.3323
01-067	3.99213	13	·	431.3	6.82	83.69	3.58	5.74	0.3494
01-044	3.99069	14	82	429.8	6.46	77.96	3.86	6.11	0.3353
01-001	3.98962	15	·	448.7	6.59	84.80	3.39	5.78	0.3343
01-111	3.98518	16	7	420.3	6.56	80.53	3.62	6.02	0.3339
01-145	3.97674	17	48	441.4	6.62	84.12	3.44	5.75	0.3329
01-166	3.97592	18	25	441.1	6.61	80.84	3.81	5.77	0.3276
01-052	3.96495	19	50	438.7	6.72	86.07	3.42	5.50	0.3352
01-089	3.95993	20	12	427.7	6.53	82.88	3.44	5.81	0.3369
01-081	3.95686	21	6	442.5	6.56	82.12	3.44	5.88	0.3362
01-053	3.94333	22	9	434.7	6.43	78.17	3.62	6.09	0.3404
01-203	3.94186	23	·	437.9	6.49	80.68	3.43	5.98	0.3552
01-040	3.92845	24	8	447.2	6.42	79.34	3.59	5.92	0.3398
01-084	3.91952	25	27	445.7	6.51	82.43	3.50	5.62	0.3390
01-078	3.91876	26	32	431.0	6.48	79.06	4.11	5.43	0.3336
01-143	3.91634	27	5	441.7	6.69	84.74	3.01	5.80	0.3275
01-187	3.91512	28	20	443.2	6.36	78.28	3.76	5.82	0.3285
01-202	3.91464	29	·	427.0	6.56	81.50	3.26	5.92	0.3240
01-093	3.91301	30	33	435.2	6.65	80.16	3.37	5.96	0.3385
01-073	3.90758	31	15	434.9	6.41	76.80	3.77	5.94	0.3360
01-012	3.90395	32	19	433.1	6.30	75.38	3.89	5.97	0.3291
01-132	3.90158	33	·	423.5	6.58	78.08	3.87	5.68	0.3388
01-031	3.89813	34	17	429.5	6.31	73.83	3.95	6.06	0.3445
01-186	3.88072	35	69	432.5	6.45	79.29	3.62	5.68	0.3264
01-070	3.87317	36	36	419.6	6.28	73.30	4.02	5.94	0.3383
01-156	3.85791	37	·	437.7	6.68	79.85	3.58	5.55	·
01-176	3.85541	38	·	432.6	6.30	74.40	3.69	6.04	0.3419
01-002	3.83901	39	·	429.7	6.63	81.03	3.18	5.70	0.3303
01-013	3.82400	40	·	442.8	6.56	81.64	3.14	5.60	0.3361
01-029	3.82051	41	18	433.2	6.34	77.04	3.59	5.68	0.3328
01-050	3.81195	42	30	416.1	6.28	70.44	3.95	6.04	0.3407
01-165	3.80736	43	·	437.3	6.73	83.53	3.31	5.16	0.3319
01-159	3.80679	44	35	435.9	6.39	76.26	3.67	5.63	0.3485
01-154	3.80405	45	11	416.6	6.41	75.87	3.66	5.67	0.3308
01-103	3.79797	46	28	430.7	6.39	75.47	3.83	5.53	0.3405
01-162	3.79589	47	29	433.3	6.34	76.46	3.34	5.86	0.3430

APPENDIX I. (Continued)

Family	Index	R10	R7[1]	HT10	DB	VO	ST	BR	WD
01-049	3.79229	48	34	413.6	6.25	72.97	3.70	5.90	0.3379
01-136	3.79137	49	42	427.8	6.18	72.89	4.12	5.52	0.3353
01-075	3.79102	50	63	423.6	6.37	75.04	3.75	5.62	0.3374
01-138	3.78555	51	54	425.3	6.44	75.44	3.87	5.44	0.3404
01-030	3.78240	52	.	440.2	6.45	80.52	3.10	5.57	0.3374
01-076	3.77969	53	.	427.0	6.29	76.15	3.57	5.61	0.3393
01-092	3.77943	54	.	428.2	6.36	73.55	3.62	5.85	0.3330
01-017	3.77828	55	72	437.3	6.25	74.88	3.41	5.89	0.3262
01-065	3.77803	56	.	417.4	6.13	67.12	4.06	6.15	0.3439
01-096	3.77711	57	57	435.8	6.34	74.24	3.70	5.69	0.3385
01-077	3.77546	58	38	421.9	6.22	70.22	3.87	5.97	0.3340
01-010	3.77132	59	46	434.9	6.31	76.20	3.62	5.52	0.3242
01-035	3.77124	60	2	420.8	6.18	72.56	3.96	5.61	0.3415
01-083	3.76978	61	.	423.4	6.30	72.11	3.44	6.13	0.3239
01-034	3.76712	62	61	436.9	6.37	77.73	3.71	5.25	0.3386
01-098	3.76618	63	77	423.6	6.38	74.09	3.62	5.73	0.3397
01-121	3.76456	64	70	429.4	6.30	74.84	3.75	5.52	0.3349
01-032	3.75570	65	31	426.4	6.32	73.56	3.73	5.64	0.3343
01-063	3.75568	66	.	431.2	6.53	78.39	3.30	5.50	0.3347
01-071	3.75489	67	52	426.8	6.13	70.55	3.99	5.73	0.3422
01-007	3.75421	68	.	434.1	6.57	79.58	3.39	5.28	0.3322
01-151	3.75285	69	59	423.3	6.34	74.29	3.66	5.61	0.3370
01-200	3.74342	70	45	413.4	6.48	73.86	3.37	5.88	0.3396
01-119	3.74239	71	.	437.3	6.32	74.69	3.56	5.61	0.3447
01-018	3.73172	72	60	419.2	6.21	69.40	3.51	6.19	0.3364
01-153	3.72487	73	41	419.1	6.23	72.94	4.00	5.32	0.3344
01-101	3.72017	74	101	418.8	5.97	65.70	4.03	6.07	0.3517
01-079	3.71410	75	66	424.1	6.31	73.43	3.69	5.50	0.3376
01-086	3.71340	76	47	415.4	6.20	71.84	3.89	5.49	0.3407
01-097	3.70937	77	.	422.4	6.30	72.43	3.47	5.79	.
01-142	3.70801	78	24	440.7	6.28	76.77	3.05	5.69	0.3322
01-109	3.70761	79	88	418.2	6.46	75.85	3.41	5.46	0.3390
01-127	3.70683	80	.	430.1	6.32	74.66	3.44	5.56	0.3422
09-019	3.70432	81	.	416.0	6.15	69.30	3.56	6.03	0.3437
01-102	3.70380	82	49	429.8	6.44	77.82	3.59	5.06	0.3424
01-120	3.70227	83	.	436.9	6.27	73.42	3.48	5.64	0.3430
01-161	3.70162	84	43	413.8	6.35	72.24	3.75	5.52	0.3363
01-014	3.70028	85	56	417.8	6.22	69.04	4.03	5.61	0.3383
01-167	3.69833	86	111	419.1	6.16	68.86	3.42	6.18	0.3387
01-174	3.69678	87	44	432.8	6.37	76.04	2.94	5.82	0.3393
01-045	3.69570	88	62	406.1	6.06	64.60	4.15	5.97	0.3359
01-080	3.68471	89	75	410.1	6.05	65.11	4.00	6.00	0.3325
01-169	3.67686	90	67	423.1	6.29	71.92	3.61	5.57	0.3486
01-113	3.67625	91	71	428.1	5.96	66.06	4.16	5.71	0.3405
01-019	3.67604	92	86	418.0	6.03	65.62	3.95	5.95	0.3442
01-148	3.67595	93	.	424.2	6.41	74.68	3.12	5.71	0.3402
01-201	3.67357	94	26	434.2	6.07	68.58	3.80	5.75	0.3460
01-123	3.67156	95	55	422.2	6.23	71.60	3.48	5.70	0.3442

APPENDIX I. (Continued)

Family	Index	R10	R7[1]	HT10	DB	VO	ST	BR	WD
01-133	3.66789	96	74	421.4	6.10	67.86	3.64	5.95	0.3470
01-062	3.66390	97	40	442.9	6.25	74.23	3.42	5.43	0.3440
01-025	3.66238	98	37	413.3	5.98	67.02	3.67	5.99	0.3353
01-168	3.65944	99	93	429.6	6.29	74.37	3.38	5.43	0.3317
01-106	3.65849	100	53	426.7	6.36	74.75	2.98	5.75	0.3405
01-008	3.65219	101	.	420.1	6.21	70.78	3.58	5.61	0.3357
01-110	3.65024	102	.	412.3	6.18	71.81	3.37	5.68	.
01-022	3.64907	103	.	395.1	5.86	60.55	4.23	6.13	0.3355
01-069	3.64655	104	22	431.2	6.20	71.69	3.06	5.96	0.3359
GLRD[2]	3.64449	105	.	430.9	6.32	73.17	3.32	5.55	0.3294
01-088	3.64132	106	39	411.5	6.19	68.92	3.51	5.83	0.3334
01-009	3.63817	107	16	431.0	6.24	72.59	3.38	5.53	0.3349
01-072	3.63762	108	107	414.0	6.26	72.16	3.33	5.62	0.3309
01-141	3.63182	109	23	426.6	5.91	68.59	3.36	5.96	0.3325
01-115	3.63042	110	79	428.4	6.14	70.68	3.44	5.65	0.3381
01-011	3.62894	111	14	430.7	6.18	72.60	3.07	5.77	0.3386
01-164	3.62668	112	.	422.5	6.09	68.31	3.62	5.73	0.3323
01-147	3.62633	113	105	410.4	6.08	65.82	3.58	6.04	0.3459
01-026	3.62286	114	68	407.0	5.99	62.31	3.68	6.32	0.3420
01-043	3.62058	115	92	399.8	6.06	64.35	3.87	5.91	0.3400
01-051	3.61944	116	64	411.3	6.22	68.96	3.56	5.68	0.3374
01-149	3.61904	117	.	403.1	6.32	71.21	3.57	5.42	0.3319
01-068	3.61767	118	80	413.4	6.00	66.59	3.52	5.97	0.3453
01-205	3.61673	119	21	414.0	6.00	64.99	3.85	5.84	0.3475
01-085	3.61129	120	108	425.6	6.21	71.03	3.63	5.35	0.3373
01-055	3.60692	121	114	405.8	5.96	62.22	3.72	6.22	0.3362
01-160	3.60570	122	109	427.2	6.17	69.60	3.48	5.62	0.3459
01-015	3.60246	123	81	424.9	6.23	71.35	3.46	5.43	0.3450
01-095	3.60034	124	87	416.1	6.30	72.23	3.19	5.57	0.3414
01-150	3.58925	125	94	409.8	6.09	66.43	3.66	5.73	0.3477
01-139	3.58660	126	110	398.1	5.97	63.32	3.77	5.96	0.3407
01-116	3.58251	127	51	424.8	6.30	72.47	2.93	5.70	0.3430
TRAC2[2]	3.58208	128	.	444.2	6.18	72.60	3.24	5.40	0.3392
01-087	3.58117	129	.	415.1	6.15	66.18	3.42	5.94	0.3448
01-066	3.57608	130	58	427.6	6.17	70.76	3.17	5.64	0.3329
01-057	3.57573	131	103	409.0	6.03	65.18	3.48	5.97	0.3396
01-020	3.57424	132	116	397.7	5.86	60.61	3.74	6.23	0.3358
01-024	3.57098	133	.	410.5	5.78	59.89	3.81	6.23	0.3412
01-155	3.57001	134	97	408.7	6.08	65.68	3.85	5.55	0.3410
01-122	3.56821	135	.	408.8	6.31	70.57	3.35	5.46	0.3473
01-033	3.54584	136	104	419.6	6.17	68.98	3.43	5.46	0.3451
01-054	3.53625	137	73	421.0	6.04	68.05	3.21	5.72	0.3352
01-104	3.53237	138	115	416.0	6.11	68.58	3.64	5.25	0.3422
01-082	3.53057	139	.	406.2	5.87	64.35	3.53	5.81	.
01-064	3.52819	140	98	405.1	6.00	64.58	3.85	5.48	0.3404
01-114	3.52542	141	90	411.5	6.11	67.22	3.78	5.24	0.3388
01-157	3.52092	142	76	418.4	6.00	65.79	3.57	5.57	0.3432
01-074	3.50629	143	84	404.7	6.04	64.52	3.41	5.79	0.3425

APPENDIX I. (Continued)

Family	Index	R10	R7[1]	HT10	DB	VO	ST	BR	WD
01-004	3.50574	144	·	412.2	5.87	62.63	3.69	5.74	0.3334
01-039	3.50037	145	99	388.7	5.88	59.71	3.49	6.22	0.3359
01-041	3.49397	146	89	399.8	5.75	57.45	3.84	6.12	0.3426
01-158	3.49289	147	83	409.9	6.25	68.31	3.40	5.32	0.3362
01-137	3.49232	148	113	408.7	5.97	64.37	3.62	5.55	0.3331
09-042	3.48361	149	·	405.5	5.81	59.55	3.71	5.96	0.3437
01-023	3.47880	150	112	395.0	5.92	61.18	3.49	5.96	0.3305
01-100	3.46650	151	106	408.4	5.92	64.13	3.52	5.55	0.3391
01-108	3.45061	152	85	415.5	5.96	63.90	3.60	5.43	0.3479
01-204	3.44794	153	78	406.8	5.86	60.71	3.61	5.76	0.3448
01-021	3.43962	154	65	393.5	5.36	50.25	4.36	6.19	0.3526
01-003	3.43008	155	96	406.6	5.92	63.59	3.36	5.59	0.3355
01-038	3.42452	156	91	394.1	5.57	52.53	3.66	6.51	0.3433
01-036	3.42073	157	·	388.7	5.77	62.04	3.15	5.91	0.3362
01-190	3.39660	158	117	414.4	5.81	60.78	3.75	5.39	0.3455
01-042	3.37722	159	102	395.0	5.78	57.01	3.79	5.68	0.3433
01-047	3.35744	160	·	386.4	6.00	55.95	3.82	5.68	0.3417
01-059	3.35300	161	95	399.8	5.81	60.38	3.46	5.50	0.3380
01-188	3.29884	162	·	412.9	5.71	60.14	3.00	5.70	·
01-189	3.26272	163	100	419.6	5.85	62.66	2.80	5.44	0.3375
01-027	3.24005	164	118	388.5	5.46	50.33	3.55	6.01	0.3401

[1]Ranking based on 118 families represented on all four sites.
[2]Reserve stand checklot.
·Data not available.

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